Opinion

The Labile Limits of Forbidden Interactions

Juan P. González-Varo [1,2,*] and Anna Traveset [3]

[1] Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

[2] Integrative Ecology Group, Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain

[3] Mediterranean Institute of Advanced Studies, IMEDEA (CSIC-IUB), Esporles, Mallorca, Spain

* Correspondence: jpg62@cam.ac.uk (J.P. González-Varo).

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Forbidden links are defined as pairwise interactions that are prevented by the biological traits of the species. Here, we focus on the neglected importance of intraspecific trait variation in the forbidden link concept. We show how intraspecific trait variability at different spatiotemporal scales, and through ontogeny, reduces the expected prevalence of forbidden interactions. We also highlight how behaviour can foster interactions that, from traits, would be predicted as forbidden. We therefore discuss the drawbacks of frameworks recently developed to infer biotic interactions using available trait data (mean values). Mispredictions can have disproportionate effects on inferences about community dynamics. Thus, we suggest including intraspecific trait variability in trait-based models and using them to guide the sampling of real interactions in the field for validation.

What are forbidden interactions and why do they matter?

Biotic interactions across trophic levels govern the dynamics of communities and the functioning of ecosystems [1-5]. Interspecies relationships not only determine energy fluxes [6], but also mediate key ecological functions such as mycorrhizal-mediated mineral nutrition [7], animal-mediated pollination and seed dispersal [8]. When sampling such interactions in the field, the norm is that certain pairwise interactions remain undetected, named the missing and forbidden links [9,10]. **Missing links** (see Glossary) are possible but hardly observable interactions, whereas **forbidden links** are pairwise interactions that are prevented by biological **traits** of the species [9,10], such as their size, morphology, phenology, physiology–biochemistry or habitat specificity. For instance, large-sized food items, like animal preys or fruits, can preclude consumption by small-gaped eaters [11-15], whereas non-overlapping phenologies impede the temporal encounter between potentially interacting species [10]. Indeed, both morphology and phenology explain a huge fraction of unobserved interactions in pollination and frugivory networks [10]. By constraining the number of possible interactions, forbidden interactions are of major importance for the

40 structure and functioning of ecological networks, including **food webs** and **bipartite networks** of mutualistic and antagonistic systems [16-22].

42 Largely motivated by the ongoing biodiversity crisis, ecologists have recently stressed the need for inferring biotic interactions at wide geographical scales [15,23-26], 44 acknowledging interactions are key for predicting species distributions in response to global change pressures [27-29]. To cope with this demand, Morales-Castilla *et al*. [24] 46 have recently presented a new conceptual framework to infer pairwise interactions in unknown systems, that is, the elements that build up complex networks of ecological 48 relationships. The framework is based on **trait matching**, particularly, on the use of available trait data (e.g. body size) to establish forbidden links [24]. A critical question that 50 arises from such predictive attempts is: how accurately can we establish forbidden links using available trait information? In other words, how reliably can we infer different types 52 of pairwise interactions using available trait data?

Here, we focus on the neglected importance of intraspecific trait variability in the 54 forbidden link concept, which is usually considered as a categorical fact (forbidden or not) rather than as a trait-matching continuum. Matching traits can vary dramatically within a 56 species across space (see Box 1), between individuals within populations and between populations within its whole distribution range [30-33]. But matching traits can vary even 58 more in time (Box 1), between years and through the ontogenetic stages of individuals. We show how intraspecific trait variability at different spatiotemporal scales reduces the 60 expected prevalence of forbidden interactions (Box 1), thereby increasing **species degree** and overall **network connectance**. We also highlight that behaviour can foster pairwise 62 interactions that would rarely be expected from trait data. Consequently, we discuss the potential limits and drawbacks of using mean values available from trait databases [34-36] 64 to infer pairwise interactions and community dynamics. Although the trait-matching

approach can be useful for elucidating general patterns within already sampled systems, we argue that it could fail to detect key interactions that allow species co-occurrences and drive critical ecological functions.

How accurately can we assign forbidden links using available trait data?

The forbidden link concept has proved useful to explain *a posteriori* interaction degree and some emergent properties of empirical networks [10,21,37]. In these analyses, forbidden links are regarded as immutable realities within the studied systems, i.e. as structural zeros in the adjacency matrices of interacting species [10,21,24]. This rigid view has probably been fostered by strong trait-matching evidence from networks in which interaction sampling was coupled with trait measurements [10,21,37]. However, it is widely recognized that empirical networks represent temporal snapshots (weeks, months, or at best a few years) of complex interactions sampled at a particular site [38]. Because traits are a suitable *post hoc* explanation of interaction patterns in these 'well-known' snapshots [37], can we then use traits to accurately infer pairwise interactions in unknown systems?

The framework proposed by Morales-Castilla *et al*. [24] relies on the use of available trait information (or phylogenetic distance as a surrogate for trait similarity if information on traits is unavailable). Global databases of **functional traits** are currently accessible for different taxonomic groups, including plants, birds, mammals, reptiles and amphibians [34-36]. These data consist of trait mean values, which should ideally represent averages for all individuals of each species across its whole distribution range. The reality is that trait means usually account for a small number of individuals measured at a particular location in a certain moment. But more limiting than their representativeness is the fact that trait means neglect the existing intraspecific variation, thus, they underestimate the degree of trait matching by overestimating the incidence of forbidden interactions (Figure 1, Box 1).

90 The latter can lead to serious misinterpretations about the dynamics and functioning of the inferred ecosystems.

92 Conspecific individuals differ in the multiple traits that produce their phenotypes. Such variability was indeed the essence for the Darwin's theory of evolution by natural 94 selection and is considered to be crucial in many ecological and evolutionary processes [39-41]. Intraspecific trait variability enhances average interaction degree of species and 96 network connectance (Figure 1, Box 1), thereby robustness to secondary extinctions [42,43]. In the following sections, we address the role of different sources of intraspecific 98 variation on the degree of trait matching between species. Moreover, we discuss the importance of behaviour in allowing interactions that would be predicted as forbidden on 100 the basis of available traits.

102 ***Matching traits vary in space and time***

The most pervasive cases of intraspecific trait variation are among-individual differences in 104 age and sex [39,44]. We specifically focus on ontogenetic trait variation in the next section, since traits and interactions can vary tremendously between individuals of different age or 106 life stage. Sexual dimorphisms typically entail differences in size or shape, which can lead each gender to interact with different species [45,46]. For instance, males and females of 108 the purple-throated carib hummingbird (*Eulampis jugularis*) feed on two different *Heliconia* species whose flowers match to the shape and length of the bill of each gender 110 [45]. In the Eurasian sparrowhawk (*Accipiter nisus*), the body size of females (185–342 g) is about double that of males (110–196 g) [47]. As a result, females prey on birds up to 150 112 g (occasionally up to 500 g), mainly thrushes (Turdidae), starlings (Sturnidae) and pigeons (Columbidae), whereas males normally prey on birds up to 40 g, including tits (Paridae), 114 finches (Fringillidae), sparrows (Passeridae) and buntings (Emberizidae) [48]. Both examples illustrate how sexual dimorphism increases intraspecific trait variability, thus,

116 interaction degree at the species level. Hence, some interactions can be forbidden for one gender but possible for the other. Yet, sex-dependent trophic niches with bimodal trait
118 distribution are reduced to a single value in trait databases: the mean.

Furthermore, intraspecific trait variability can also be huge among individuals of the
120 same sex and age. Species traits vary in space at different hierarchical levels or spatial scales [30,32,33], among individuals within populations and among populations across the
122 species ranges (see Figure I in Box 1). In the case of plants, traits even vary within the same individual (see Figure II in Box 1), among leaves, flowers and fruits, organs that mediate
124 several interactions with different types of feeding animals (herbivores, pollinators, florivores, seed dispersers and seed predators) [31,49]. Phenotypes result from the
126 interaction between individuals' genes and local environmental conditions, each source of variation having a specific relative weight in determining the expression of different traits
128 [50]. Therefore, those traits that strongly depend on the local environment are prone to vary in time, between phenological events under different climate conditions (Box 1). For
130 instance, water deficits reduce the size and alter the chemical composition of fruits [51]. Consequently, these traits can hugely vary between consecutive years even in the same
132 individual plant, thus, in the same population, which increases uncertainty even when using local trait data to infer local interactions (Box 1). Despite its importance, intraspecific trait
134 variability in time has been largely overlooked in community ecology [25,41].

Regardless of whether the main source of variation is genetic or environmental, trait
136 variability makes individuals of a given species (or plant organs) non-interchangeable from the perspective of their interacting partners (see Figure II in Box 1). Actually, different bird
138 species have been reported to consume fruits of specific size distributions within the same plant species according to their gape widths [13,52]. Similarly, different flower visitors and
140 herbivores have been documented to visit different individual plants according to their

flowering phenology, morphology and flower scent [53]. At the species level, the result of particular individuals (or plant organs) interacting with particular partner species is an increase in the possibilities of trait matching (see Figure II in Box 1), that is, a broader 'interaction niche' generated by between-individual niche differences [39]. Whenever inheritable, such differences can also be the basis of evolutionary changes after the loss or gain of partner species [13].

Conversely, a framework that uses trait means to infer biotic interactions assumes that all individuals, thereby all populations, are interchangeable. This assumption can lead to important predictive errors associated to (*i*) the representativeness of available trait data and (*ii*) the neglect of intraspecific variation. First, trait means account for individuals sampled in one or a few locations during a particular moment. How well do these subsets represent a species average across its entire distribution? For example, mean diameter in myrtle (*Myrtus communis*) fruits can range from 7.3 to 10.4 mm, depending on which population and year the fruits were sampled (see Figure I in Box 1). Hence, using a trait mean obtained at a particular 'site–year' combination to infer interactions at different locations can lead to under- or overestimation of forbidden links, depending on the sign of the extrapolation error (e.g. from population L to M or vice versa; Figure I in Box 1). Secondly, using trait means raises concerns about the predicted prevalence of forbidden interactions when neglecting intraspecific variability. In the same example, myrtle fruits are predicted as fully prevented for Sardinian warblers (*Sylvia melanocephala*) when using mean diameters as interaction threshold, but such interaction is expected across myrtle populations when using minimum values as threshold (see Figure I in Box 1). Accordingly, there is empirical evidence that, indeed, Sardinian warblers regularly consume myrtle fruits in different regions [10,54,55]. The myrtle and the Sardinian warbler are common and locally abundant species in the studied sites, and abundance is a critical factor promoting

166 both the establishment and strength of interactions through increasing interspecies encounter rates [25,56], even when such interactions are predicted to be unlikely from
168 traits.

170 ***Ontogeny enlarges intraspecific trait variability***

Traits can hugely vary between the life stages of one species, which promotes stage-
172 specific interactions [44,57]. The first life stage of most organisms (e.g. seeds in plants, and eggs or newborn in animals) is normally tiny compared to adults. Thenceforth, ontogeny
174 normally entails an increase in body size, thereby an allometric shift of interacting partners [12,57-59]. Keeping species roles as predators and prey, ontogeny not only allows young
176 prey individuals to be consumed by smaller predator species (e.g. Figure 2a), but also adult and young predator individuals to feed on different prey species according to their size
178 [12,14,58,59]. Therefore, ontogeny generates a broader niche space for both consumers and resources, allowing interactions that would be assigned as forbidden if we only look at the
180 adult traits. Besides, individuals of some species can increase in weight by several orders of magnitude during their life, shifting their role from being a prey of certain species to being
182 a predator of another species (Figure 2b). These vast shifts can promote reciprocal predation among species of the same trophic level and even cannibalism [14,57,59,60]. For
184 instance, an egg of Nile crocodile (*Crocodylus niloticus*) weights ~0.1 kg while an adult typically exceeds 200 kg, i.e. four orders of magnitude larger [61,62]. Ontogenetic variation
186 allows animals of ca. 1–10 kg such as monitor lizards (Varanidae), herons (Ardeidae) and ravens (Corvidae) to prey on the eggs and juveniles of this apex predator (Figure 2a), with
188 profound effects on its demography [61,63]. Interestingly, ontogeny can reverse the direction of predation when adult predators can feed on those species which predate on
190 their early life stages, leading to feeding loops (Figure 3). Such loops are remarkably common and can be of major importance for community dynamics [14,57,59,60].

192 It is not difficult to envisage that ontogenetic variability can generate an enormous uncertainty when attempting to predict biotic interactions using available trait means of
194 adult individuals, which might lead us to wrong inferences about community dynamics. For instance, reciprocal predation through life-stage-specific interactions promotes coexistence
196 between native Mohave tui chub (*Siphateles bicolor mohavensis*) and invasive western mosquitofish (*Gambusia affinis*) [14]. Gravel *et al*. [26] have recently proposed
198 distinguishing 'subspecies' by size (ontogenetic) categories to build trait-based networks, which would describe more accurately those pairwise interactions involving species with
200 size structured populations. A major limitation to this approach is the lack of available trait data for species' life-stages other than the adult [34-36].

202

Behaviour can allow 'forbidden' interactions

204 Species interactions that initially appear unlikely can eventually be established at ecological timescales through changes in animal behaviour. Animal innovations (i.e. animals behaving
206 in an innovative way) have been described in a number of taxa, particularly in resource-poor or novel environments [64]. For example, Laland & Reader [65] found that food-
208 deprived guppies (*Poecilia reticulata*) are more likely to develop foraging innovations than non-food-deprived individuals. Tinker *et al*. [66] found analogous results in California sea
210 otters (*Enhydra lutris nereis*) at a resource-limited site, where individuals specialized on different preys by acquiring specific behavioural skills. Birds are especially innovative in
212 their foraging techniques [67] and recent experiments have demonstrated that the information can spread rapidly among individuals in the population through social network
214 ties [68]. The kelp gulls (*Larus dominicanus*) at Peninsula Valdés provide an excellent example. In the 1970s, kelp gulls began to feed on skin and blubber of living southern right
216 whales (*Eubalaena australis*) by pecking on their backs [69]. Since then, the percentage of living right whales (mothers and calves) with gull lesions has increased from 2% to 99% in

218 the 2000s, and wounding is now considered a major cause of whale mortality [70]. The gull population grew rapidly in the last decades parallel to the human population on the nearby
220 mainland [69]. Rapid population growth is a common feature of biological invasions, and this example shows that the outcomes can be surprising in terms of interspecies
222 interactions. Even more unexpected is the emergence of interactions between the sharp-beaked finch (*Geospiza difficilis*) and different booby species (*Sula* spp.) on the small,
224 isolated and food-limited islands of Wolf and Darwin (see Figure 2c). This finch feeds on insects and small seeds in the Galapagos Islands, but on Wolf and Darwin the so-called
226 vampire finch also feeds on the blood and eggs of these seabirds [71]. Information on bill traits alone would rarely predict this strange but critical interaction for the sharp-beaked
228 finch at the extreme of the archipelago.

Besides promoting interactions, behaviour can also modify the sign of pairwise
230 interactions, from mutualistic (positive) to antagonistic (negative) or vice versa, leading to partner dualities. For instance, scatter-hoarding birds and mammals are seed predators but
232 they also provide effective seed dispersal by moving caches that are eventually forgotten or released if the animal dies [72]. In the Neotropics, agoutis (*Dasyprocta punctata*) are
234 actually claimed to have been responsible for the persistence of large-seeded species that were once dispersed by megafauna which went extinct more than 10,000 years ago [73]
236 (Figure 2d). It is not always simple to foresee in which cases an animal species will behave as a mutualist or antagonist, but we must bear in mind that such changes in the sign of
238 interactions can have important implications for community dynamics.

240 Concluding Remarks and Future Directions

The thresholds delimiting forbidden interactions are labile as a result of intraspecific trait
242 variability, which can be substantial. We have illustrated that only using available trait data

(i.e. means) underestimates species degree (thus, network connectance) through overestimating the incidence of forbidden links. Also, that available trait means might not be representative across the species ranges, which can lead to both over- and underestimations of interactions inferred locally. Recently developed probabilistic models now allow incorporating intraspecific trait variability to predict interactions [26,56]. However, the challenge to accurately infer biotic interactions in unknown or novel ecosystems is to gather detailed trait data for multiple species, well replicated across their ranges and ontogenetic stages, and then, to make these data available alongside descriptive statistics of intraspecific trait variability. Although promising, this enterprise is clearly colossal. Alternatively, one could quantify intraspecific trait variability in well-sampled species (e.g. Box 1) and transfer an equivalent amount of variance to taxonomically or phylogenetically close species lacking such detailed data (see Outstanding Questions). In sum, we recommend incorporating intraspecific trait variability in models predicting networks of biotic interactions.

Even with detailed trait information available, there are still many sources of uncertainty affecting the establishment of pairwise interactions. On the one hand, predicted but not recorded interactions (false positives) could reflect mismatches in non-morphological or phenological traits (such as physiology or biochemistry), or reflect cognitive constraints, which can block the formation of inferred interactions [e.g. 74]. On the other hand, in novel scenarios, behavioural innovation can promote interactions predicted as forbidden (false negatives). Evidence shows that these 'outliers' matter, especially when they affect common or keystone species with a disproportionate role in community dynamics and ecosystem functioning (see Outstanding Questions).

It is therefore essential to be aware that reducing the enormous complexity behind biotic interactions to trait-matching models can critically limit our inferences. Yet, inferred

268 networks might serve as ‘maps’ to guide sampling of real interactions. Particularly, they could help to focus sampling effort on predicted links (included the forbidden ones) that
270 seem to be key for the target communities, in order to validate network-model predictions (see Outstanding Questions). Novel techniques (e.g. DNA barcoding, GPS tagging, camera
272 trapping) are now revolutionizing the sampling of biotic interactions, unravelling unprecedented information about the functions they entail [52,73,75]. We thus need
274 synergies between trait-based models and empirical studies if we are to understand how interspecies relationships shape the fate of communities and ecosystems.

276

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Figure 1. Frequency Distribution of Matching Traits (e.g. Body Size or Phenology) in a Consumer and a Resource Species. Interaction is possible whenever $x_{consumer} \geq x_{resource}$. (a) Mismatching between both trait means and intraspecific variability prevent interaction, leading to a totally forbidden link. (b) Mismatching occurs between trait means but intraspecific variability allows interaction, leading to a partially forbidden link. The difference between (a) and (b) – thus, our ability to infer interactions – may depend on how broadly intraspecific trait variability has been assessed in space and time (see Box 1).

Figure 2. Examples of How Ontogenetic Variability and Behaviour Promote Interspecific Interactions or Change their Sign. (a) Small groups of golden jackals (*Canis aureus*), which are two orders of magnitude smaller than an adult blue wildebeest (*Connochaetes taurinus*), can hunt wildebeest calves [62]. (b) The Nile monitor (*Varanus niloticus*), three orders of magnitude smaller than an adult Nile crocodile (*Crocodylus niloticus*), is the main predator of crocodile eggs [61]. (c) The Galápagos sharp-beaked finches (*Geospiza difficilis*) mainly feed on insects and small seeds, but on the small and food-limited islands of Wolf and Darwin, they cut wounds on seabirds (boobies *Sula* spp.) to drink their blood; they also push and roll seabird eggs into rocks to break them and feed on them [71]. (d) The Central American agouti (*Dasyprocta punctata*), a seed predator (antagonist) of the black palm (*Astrocaryum standleyanum*), can effectively disperse its seeds through scatter-hoarding, acting as a mutualistic partner [73]. Photos reproduced with permission from Todd Gustafson (a), Anup Shah (b), Pete Oxford (c) and Christian Ziegler (d).

Figure 3. Feeding Loop Generated by Ontogenetic Reversal of Predation. Arrows, from prey to predator, denote predation. (a) Species level diagram showing reciprocal predation between species *j* and *k*. (b) Life-stage level diagram showing how reciprocal predation is mediated by stage-specific interactions between both predators during their ontogeny: species *j* is a prey of species *k* during its earlier life stages, but it becomes a predator of species *k* in the adult stage. We could hardly infer the role of species *k* as predator of species *j* using trait data of adult individuals (e.g. body size).

Box 1. Spatiotemporal variation in trait matching

Assessing spatiotemporal variation in size matching between the fruits of the Mediterranean myrtle (*Myrtus communis*) and the gape of the five most abundant frugivore species in Circum-Mediterranean woodlands during fruit ripening (see details in Appendix S1). We assess variation in fruit diameter among populations and years across the distribution range of the plant (Figure I), and among individual plants and between consecutive years within three of these populations (Figure II) (see sections A and B, respectively, in Appendix S1). A gape width smaller than a fruit diameter involves the incapability of the frugivore to swallow the fruit [11,13], and thus a forbidden interaction. However, different forbiddance thresholds in fruit diameter – mean, first quartile (Q_{25}), 5th percentile (P_{05}) or minimum – can lead to different prevalences of forbidden interactions. These thresholds represent the capability of an average individual of each frugivore species (mean gape width) to consume fruits of average size (mean), or to consume at least 25% (Q_{25}), 5% (P_{05}), or some (minimum) of available fruits. We use this mixed and conservative approach, using mean values for the frugivores but intraspecific variability for the plant [41], owing to the lack equivalent geographical variation for gape width data [10,76-78] (see section C in Appendix S1). We show how fruit diameter varies geographically and temporally, among populations and between years within populations (Figure I). Due to geographical variation (15% variance), some populations are predicted as forbidden for narrow-gaped frugivores while others do not (Figure I). But due to interannual variation (22% variance), some populations are predicted as forbidden some years but not others (e.g. populations D and M in Figure I). We also show how forbidden links largely drop when using less restrictive thresholds. For example, when using mean fruit diameter as threshold, *S. melanocephala* results a forbidden frugivore in 100% of population-year combinations, but only in 26% when using the minimum diameters (Figure I). Accordingly, empirical information from different frugivory studies shows that all five species – even those with the smallest gape widths – actually consume myrtle fruits in different sites [10,54,55].

Figure I

Similarly, we show how fruit diameter varies among individuals within populations and between consecutive years (Figure II). Due to among-individual variation (56% variance), some plants are predicted as forbidden for narrow-gaped frugivores while others do not. But due to interannual variation (31% variance), some plants are predicted as forbidden some years while not in others (Figure II). Again, the prevalence of forbidden links depends on the forbiddance thresholds chosen (Figure II).

Figure II

Figure I. Geographical and Temporal Variation in Trait Matching. (a) Boxplot (median, quartiles and 5^{th}/95^{th} percentiles) showing variation in fruit diameter across 18 populations of Mediterranean shrub *Myrtus communis*, some of them sampled in different years (27 population-year combinations) (Appendix S1). Black dots denote means. White dots denote minimum values. Horizontal lines denote the mean gape width (mm) of the five most abundant frugivore species in Circum-Mediterranean woodlands during the winter (*Er: Erithacus rubecula*; *Sa: Sylvia atricapilla*; *Sm: Sylvia melanocephala*; *Tm: Turdus merula*; *Tp: Turdus philomelos*), period when *M. communis* ripe its fruits. (b) Map of the Mediterranean Basin with the location of the study *M. communis* populations. The distribution of *M. communis* is shown in dark-grey (redrawn from Migliore *et al*. [79]).

Figure II. Intra- and Interindividual Variation in Trait Matching. Boxplot showing variation in fruit diameter among marked myrtle plants in two consecutive years (grey and white boxes, respectively) and in three different populations. Black dots denote means. Grey and white dots denote minimum values. Horizontal lines denote the mean gape width (mm) of the five most abundant frugivore species in Mediterranean woodlands during the winter (bird species acronyms as in Figure I).

Glossary

Bipartite network: ecological network comprising two trophic levels (e.g. host and parasitoids, plants and pollinators, or plants and frugivores) with the links between species representing trophic interactions (i.e. fluxes of matter and energy) and ecological functions (e.g. pollination, seed dispersal) [8,9].

Connectance: the fraction of pairs of species that interact in an ecological network [42,80]. In food webs, $C = L/S^2$, where L is the number of interactions (links) and S the number of species in the community. In bipartite networks, $C = L/S_rS_c$, where S_r and S_c are the number of species in each trophic level (resources and consumers; e.g. plants and pollinators).

Food web: ecological network comprising multiple trophic levels (e.g. primary producers, herbivores, predators, detritivores) with the links between species representing trophic interactions (i.e. fluxes of matter and energy) [17].

Forbidden link: pairwise interaction that is prevented by the biological traits of the species [9,10].

Functional trait: any trait affecting, directly or indirectly, the performance and fitness of individuals [41].

Missing link: possible but hardly observable pairwise interaction (e.g. between rare species), thus, a result of under-sampling [10].

Species degree: the number of different species a certain species interacts with in an ecological network [9,42].

Trait: any morphological, physiological, phenological or behavioural feature measurable at the individual level [41].

Trait matching: phenotypic expression of functional traits that allow a particular interspecific interaction (Figure 1).

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Figure I – Box 1

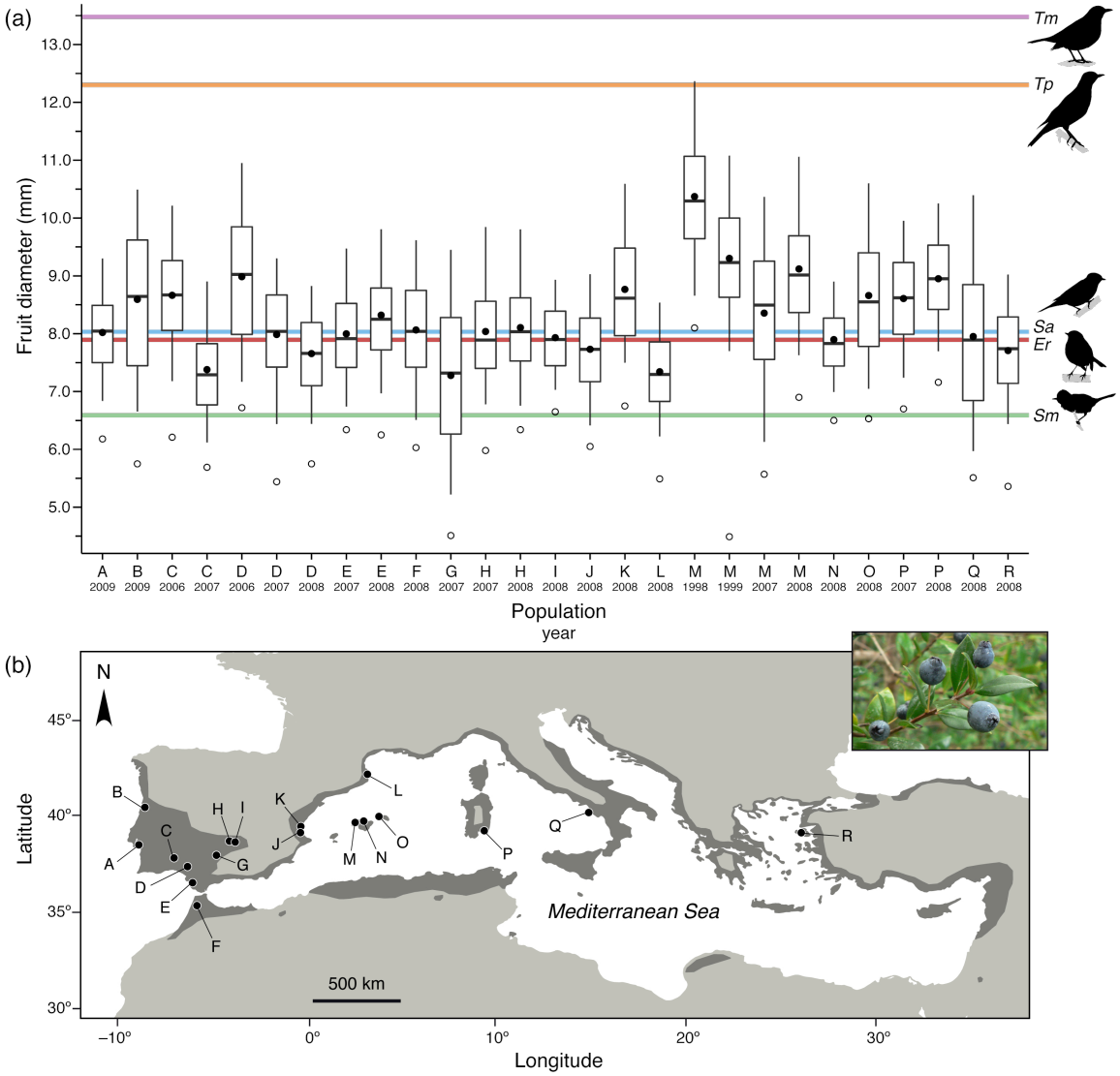

Figure II – Box 1

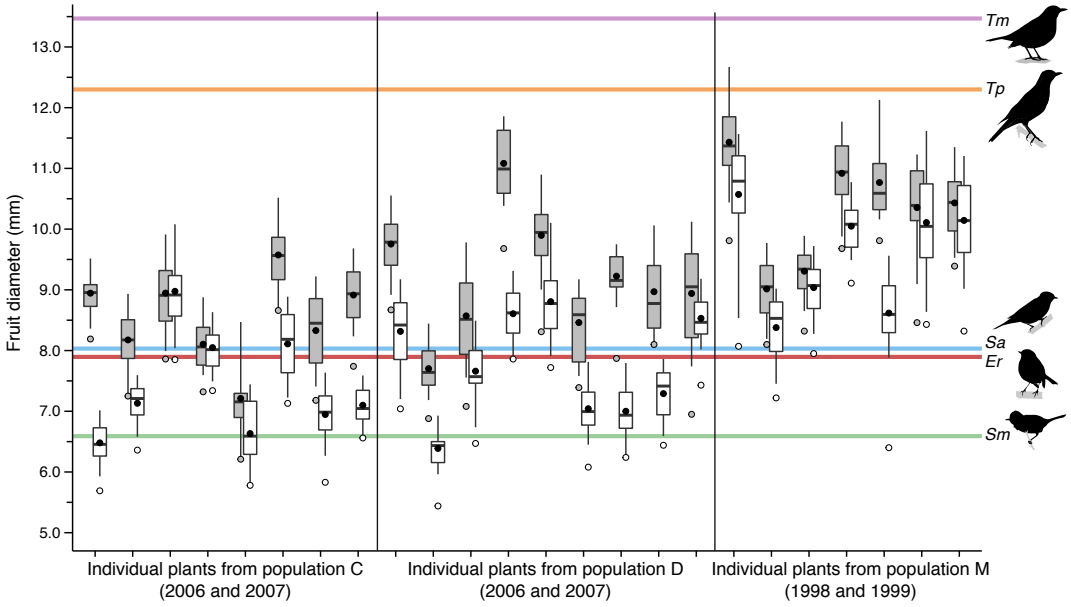

Figure 1

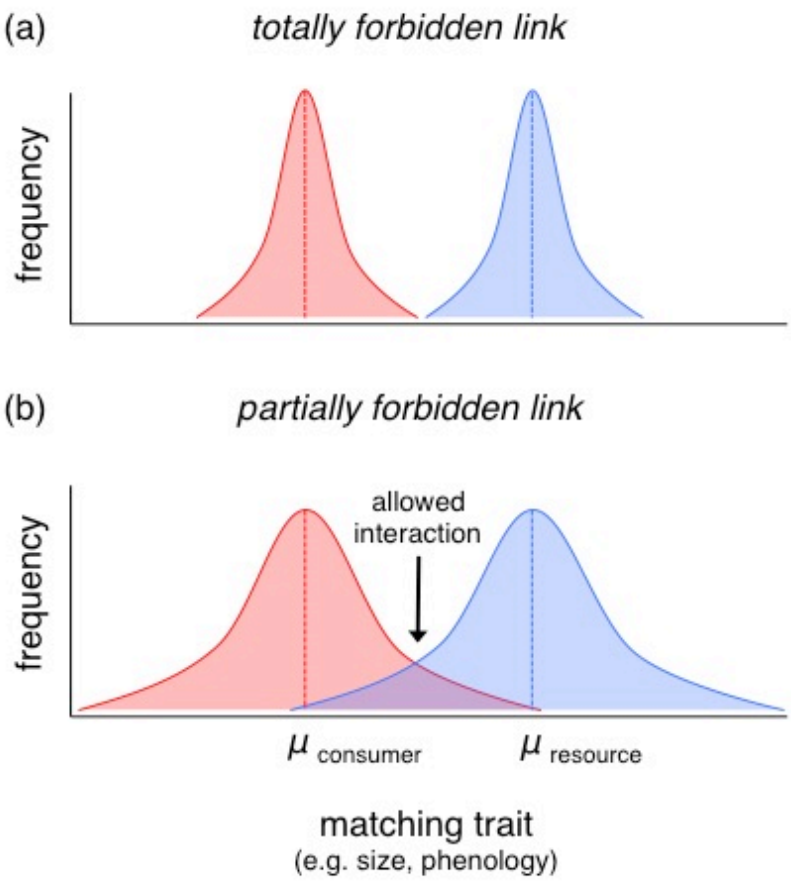
(a)
totally forbidden link
frequency
(b)
partially forbidden link
frequency
allowed
interaction
μ consumer
μ resource
matching trait
(e.g. size, phenology)

Figure 2

Figure 3